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Gitelson, Anatoly A. and Gamon, John A., "The need for a common basis for defining light-use efficiency: Implications for productivity estimation" (2015). *Papers in Natural Resources*. 483.

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The need for a common basis for defining light-use efficiency: Implications for productivity estimation

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Abstract

A primary focus of this short communication is to show how the operational definition of light use efficiency (LUE) influences the results and interpretation of the LUE model. Our study was motivated by the observation that multiple LUE definitions are reported in the literature. The temporal behavior of three operational definitions of LUE, based on (i) incident radiation, (ii) total absorbed radiation and (iii) radiation absorbed by photosynthetically active/green vegetation was examined for two contrasting crops (soybean and maize) having different physiologies, leaf structures and canopy architectures. Over the course of a growing season, the behavior of these three contrasting LUE definitions was strikingly dissimilar, and the degree of dissimilarity varied with contrasting crops (corn and soybean). This demonstrates that LUE model behavior would vary strongly with the LUE definition used, with resulting implications both for the estimated seasonal productivity, and for the interpretation of the underlying mechanism. Based on these findings, we recommend a standard definition of the LUE model based on radiation absorbed by green vegetation. We also discuss the practical and theoretical implications of using this simple conceptual model on a dynamic biological system.

Keywords: Absorbed radiation; Light use efficiency; Gross primary production

1. Introduction

The LUE model originated with the work of Monteith (1972, 1977) and has since been adopted by many in the remote sensing and carbon flux communities. While it can be viewed as a conceptual model, the LUE model can also be expressed in explicit, mechanistic terms, based on the underlying physical and physiological processes of light absorption and conversion. Conceptually, the amount of photosynthesis or primary production is largely determined by the amount of photosynthetically active radiation (PAR) absorbed by vegetation (APAR). This is further modified by the efficiency with which this absorbed light is converted to fixed carbon, light use efficiency (LUE). Loosely speaking, the absorbed radiation relates to vegetation structure and pigment pools, and the efficiency term relates to physiology. In reality, the absorption and efficiency terms can be confounded to varying degrees depending on the underlying dynamic biological processes, and on the exact operational definition of APAR and LUE.

Mechanistically, the APAR term is affected by a number of factors that include PAR irradiance, canopy structure and photosynthetic pigment content, including leaf area index (LAI), leaf angle distribution, and PAR absorptance. This absorption term tends to vary slowly over long (seasonal) time spans and is affected by the growth and senescence of vegetation, and can also be influenced over the short term (e.g. diurnally) via changing leaf display in the

case of plants exhibiting leaf movement, leaf wilting, or chloroplast movement (Björkman & Demmig-Adams, 1994). The efficiency term is affected by a number of processes that affect the energy distribution within the photosynthetic system, ranging from pigment composition (chlorophyll and carotenoid content, and the relative levels of xanthophyll cycle pigments), to enzyme kinetics (e.g. xanthophyll cycle de-epoxidase) (Björkman and Demmig-Adams, 1994; Gamon and Qiu, 1999). Together, these comprise the physiological response, which varies dynamically over short (diurnal) and long (seasonal) time scales, based on changing environmental conditions and ontogeny.

While we often think of APAR and LUE as distinct aspects of the model operating over different time scales, they are also linked in several ways, and this relationship may vary with the exact definitions used and the dynamics of changing structure and physiological state as a plant grows. The underlying explanation for this linkage lies in the tendency for plants to follow coherent rules of resource acquisition and distribution. For example, nitrogen constraints not only limit photosynthetic physiology, but also ultimately limit plant growth, resulting in coherence between plant physiological performance (affecting LUE) as well as leaf and plant structure and pigment content (affecting light absorption). This coordinated response, has been called *functional convergence*, provides a useful framework for understanding plant optical behavior (Field, 1991; Ollinger, 2010). The beauty of the LUE model is that it can be parameterized

with metrics that are widely available from remote sensing and other sources (e.g. meteorological stations). The challenge is that the measurements can only approximate the complex and dynamic system that they are meant to represent.

One of the difficulties of the LUE model is that various operational definitions exist for its component terms. For example, the APAR term can be measured on the basis of incident irradiance, absorbed irradiance, or the irradiance absorbed only by green (photosynthetically active) vegetation. This variation typically results from the different measurement approaches at different sites, which range from simple PAR irradiance (PPFD), to total PAR absorbed ($PPFD \times fPAR$), to PAR absorbed by green vegetation ($PPFD \times fPAR_{green}$). Similarly, LUE has been defined in the plant physiological literature as the initial slope (quantum yield) of the light response curve (Björkman, 1981), whereas in remote sensing literature as the carbon uptake (variously defined as the photosynthetic rate, the gross primary production, GPP, or the net primary production, NPP) divided by the irradiance (variously defined as one of the three ways described above). Additionally, while some models infer a constant LUE for all vegetation (Myneni, Los, & Asrar, 1995), some vary the LUE based on an assumed (fixed) LUE value for each vegetation type (Ruimy, Saugier, & Dedieu, 1994), and others allow LUE to vary dynamically with vegetation type and stress level as affected by internal or external (environmental) factors (Potter et al., 1993; Prince and Goward, 1995; Running et al. 2004). These differences are often defined by operational challenges that force the usage of a particular tractable definition, regardless of whether that definition is theoretically optimal.

Here we argue that the lack of standard definitions limits our understanding of mechanism, and confounds comparative analyses (meta-analyses) across studies and ecosystems. We discuss the implications of various LUE definitions and present recommendations emerging from this analysis.

There are at least three commonly used definitions of photosynthetic LUE based on: (a) incident radiation (LUE_{inc}); (b) total absorbed light (LUE_{total}); and (c) radiation absorbed by photosynthetically active vegetation (LUE_{green}) (e.g., Garbulsky, Peñuelas, et al., 2010; Hall et al., 1992; Lindquist et al., 2005; Nichol et al., 2000; Norman and Arkebauer, 1991; Suyker et al., 2004). Consequently, LUE values reported do not have a common basis, bringing confusion and limiting the utility of reported LUE values for comparative analyses. Not surprisingly, the value of LUE reported in the literature varies by a factor of three (Garbulsky, Peñuelas, Gamon, Inoue and Filella, 2010; Nichol et al., 2000; Norman and Arkebauer, 1991; Peng et al., 2011; Rosati and Dejong, 2003; Suyker et al., 2004). Similarly, the Photochemical Reflectance Index (PRI), which is sometimes considered as a proxy of LUE (Gamon, Peñuelas, & Field, 1992), has different operational definitions, resulting in a wide range of reported values for comparable conditions (Garbulsky, Peñuelas, Gamon, et al., 2010). This is further confounded by variation in the responses of optical sensors from different instruments and manufacturers; true standards in instrumentation are lacking (Balzarolo et al., 2010; Gamon et al., 2006; Gamon et al., 2010).

The initial objective of this short communication was to investigate the seasonal behavior of each definition of LUE in two contrasting crops (soybean, a C3 species; and maize, a C4 species) having different physiologies, leaf structures and canopy architectures. In both crops, green leaf area index (LAI) was closely tied to the seasonal dynamics of gross primary production (GPP), providing a simple experiment examining how the behavior of the LUE model varied depending upon how the APAR and LUE terms were defined. Consequently, a primary focus was the effect of the operational definition of LUE on the results and interpretation of the LUE model. In particular, we examined the consequences of incorporating canopy structure (and green canopy structure) into

the APAR term for the behavior of both APAR and LUE. We then discuss the practical and theoretical implications of using these different versions of this simple conceptual model on a dynamic biological system. The ultimate goal of this analysis is to draw attention to the need for standard operational definitions within the remote sensing community when using the LUE model.

2. Methods

The study took place during the growing seasons of 2001 to 2008 at a University of Nebraska-Lincoln research facility located 58 km northeast of Lincoln NE, U.S.A., and consisted of three agricultural sites; the first two were 65-ha fields equipped with center pivot irrigation systems. The third site was of approximately the same size, but relied entirely on rainfall. Site 1 was under continuous maize, while sites 2 and 3 had been under maize-soybean rotation. Soils of the study area are deep silty clay loam (Suyker et al., 2004).

Each study site was equipped with an eddy covariance tower and meteorological sensors, with which the continuous measurements of CO_2 fluxes, water vapor and energy fluxes were obtained every hour. Daytime net ecosystem exchange (NEE) values were computed by integrating the hourly CO_2 fluxes collected during a day when PAR_{in} exceeded $10^{-3} MJ/m^2/s$. Daytime estimates of ecosystem respiration (Re) were obtained from the night CO_2 exchange-temperature relationship (e.g., Xu & Baldocchi, 2003). The GPP was then obtained by subtracting Re from NEE as: $GPP = NEE - Re$. Daily GPP values were presented in the units of $gC/m^2/d$, and the sign convention used here was such that CO_2 flux to the surface was positive so that GPP was always positive and Re was always negative (details are in Verma et al., 2005).

Daily measurements of photosynthetically active radiation (PAR) were obtained using the following procedures: incoming PAR (PAR_{inc}) was measured with point quantum sensors (190-SB LI-COR, Lincoln, NE) pointing to the sky, and placed at 6 m from the ground. PAR reflected by the canopy and soil (PAR_{out}) was measured with the LI-COR point quantum sensors pointing down, and placed at 6 m above the ground. PAR transmitted through the canopy (PAR_{transm}) was measured with line quantum sensors (LI-191, LI-COR, Lincoln, NE) placed at about 2 cm above the ground, looking upward. PAR reflected by the soil (PAR_{soil}) was measured with LI-COR line quantum sensors placed about 12 cm above the ground, looking downward (details by Hanan et al., 2002 and Burba, 2005). Daily absorbed PAR (APAR) was computed by integrating the hourly PAR values collected during a day when PAR_{in} exceeded $10^{-3} MJ/m^2/d$ and calculated as (Goward & Huemmerich, 1992):

$$APAR = PAR_{inc} - PAR_{out} - PAR_{transm} + PAR_{soil}$$

$$fAPAR \text{ was calculated as } APAR/PAR_{inc}$$

To obtain a measure of the $fAPAR$ absorbed only by the photosynthetic component of the vegetation, we calculated $fAPAR_{green} = fAPAR \times (\text{green LAI}/\text{total LAI})$ (sensu Hall et al., 1992 and Hanan et al., 2002).

Within each of the study sites, six small (20 m \times 20 m) plot areas were established for detailed process-level studies. These intensive measurement zones (IMZ) represented all major occurrences of soil and crop production zones within each site. Plant populations were determined (by counting plants) for each IMZ. On each sampling date, plants from a 1 m length of either of two rows within each IMZ were collected and total number of plants recorded. Collection rows were alternated on successive dates to minimize edge effects on subsequent plant growth. Plants were transported on ice to the laboratory. In the lab, plants were dissected into green leaves, dead leaves, stems, and reproductive organs. The green leaves were run through an area meter (Model LI-3100, Li-Cor, Inc., Lincoln NE) and the leaf area per plant was

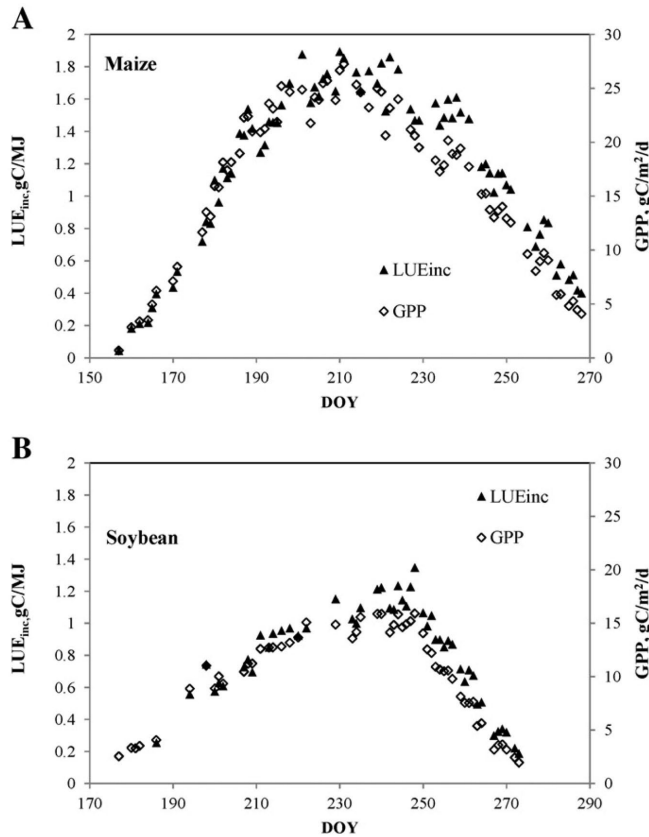


Figure 1. GPP and LUE_{inc} plotted versus day of year (DOY) for (A) maize and (B) soybean.

determined. For each IMZ, the green leaf area per plant was multiplied by the plant population (# plants m^{-2}) to obtain a green LAI. Green LAI at the six IMZs was averaged to obtain a site-level value.

LUE based on *incident radiation* was calculated as a ratio of daily gross primary production, GPP, and daily averaged incident PAR (e.g., Barton and North, 2001, Nichol et al., 2000 and Suyker et al., 2004):

$$LUE_{inc} = GPP / PAR_{inc} \quad (1)$$

LUE based on *total radiation* absorbed by vegetation was calculated as (Monteith, 1972, Norman and Arkebauer, 1991, Lindquist et al., 2005 and Kergoat et al., 2008):

$$LUE_{total} = GPP / fAPAR \times PAR_{inc} \quad (2)$$

where $fAPAR$ is fraction of daily PAR absorbed.

LUE based on PAR *absorbed by photosynthetically active, green vegetation* was calculated as (Gitelson, Peng and Huemmrich, 2014 and Hall et al., 1992):

$$LUE_{green} = GPP / fAPAR_{green} \times PAR_{inc} \quad (3)$$

$fAPAR_{green}$ was calculated in accord with Hall et al. (1992) as:

$$fAPAR_{green} = fAPAR \times (\text{green LAI} / \text{total LAI}) \quad (4)$$

3. Results and discussion

3.1. LUE_{inc}

The temporal behavior of LUE_{inc} and GPP in maize is shown in Figure 1A. LUE_{inc} was closely related to GPP, which, in turn, was closely followed by green LAI (Figure 2A) and canopy chlorophyll content (not shown, Gitelson et al., 2006 and Gitelson,

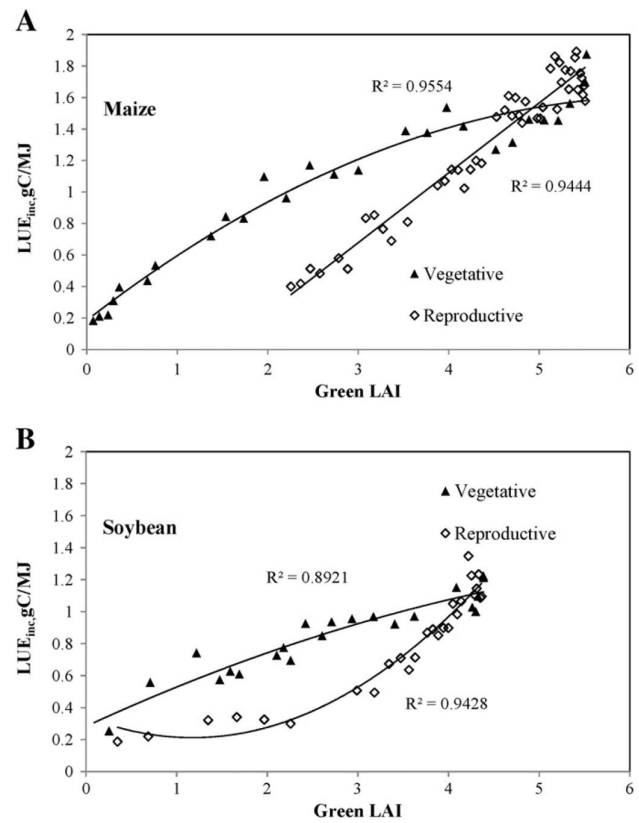


Figure 2. LUE_{inc} vs. green LAI in vegetative and reproductive stages for (A) maize and (B) soybean.

Peng, Arkebauer and Schepers, 2014). Thus, LUE_{inc} provided a close proxy of green LAI and total Chl content, although this relationship shifted between vegetative and reproductive stages (Figure 2A).

In general, the same pattern of LUE_{inc} was observed in soybean (Figure 1B). The relationship between LUE_{inc} and green LAI remained quite close during the vegetative stage, but in the reproductive stage it became essentially non-linear, with periods of almost invariable LUE_{inc} while green LAI decreased drastically in late senescence stage (Figure 2B). From these observations, it is clear that LUE_{inc} would necessarily tend to follow canopy photosynthetic capacity, primarily because it directly incorporates green canopy structure and light absorption and confounds this with the effects of changing physiology. Combining this with $fAPAR$ would “double count” the effects of green canopy structure, and is mechanistically unsound. Despite this limitation, LUE is often reported this way in the literature (e.g., Gilmanov et al., 2014; Rosati and Dejong, 2003; Suyker et al., 2004).

3.2. LUE_{total}

In both maize and soybean, the fraction of total absorbed PAR increased as vegetation fraction and green LAI increased (Figure 3) up to the point when both vegetation cover and $fAPAR$ reached maximal values. In the reproductive stage, maize $fAPAR_{total}$ remained almost invariant up to the end of growing season (Figure 3A), while $fAPAR_{total}$ of soybean decreased in the late reproductive and senescence stages (Figure 3B). Thus, LUE_{total} was much higher than LUE_{inc} in both crops in the vegetative stage, from early- to mid-season (Figure 4). Then this difference relaxed in the reproductive and senescent stages, along with the decrease of GPP and green LAI.

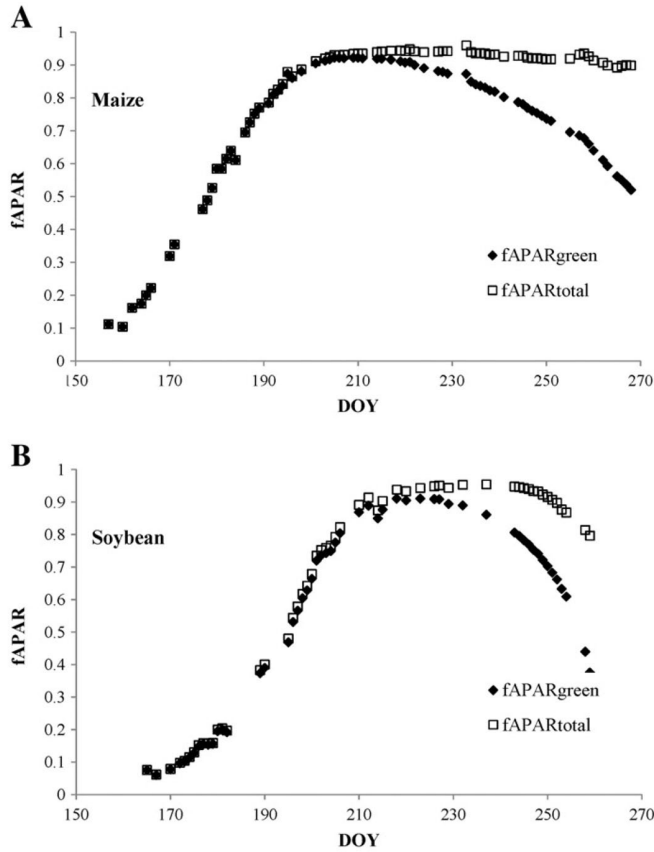


Figure 3. $fAPAR_{total}$ and $fAPAR_{green}$ versus day of year (DOY) for maize (A) and soybean (B).

LUE_{total} is a common expression of LUE in field studies incorporating measurements of canopy light absorption that do not distinguish the contribution of green from brown/yellow components to the overall absorption (e.g., Garbulsky, Peñuelas, et al., 2010; Garbulsky, Penuelas, Gamon, Inoue and Filella, 2010; Nichol et al., 2000; Norman and Arkebauer, 1991). This separation is a tedious process, and is often avoided or assumed to be negligible, but our analysis here suggests that this LUE definition may also be mechanistically incorrect in that it tends to confound varying contributions of green and brown/yellow tissues, which change over time, particularly during reproductive and senescence stages (Figure 4).

3.3. LUE_{green}

The fraction of PAR absorbed by green vegetation increased (Figure 3) as vegetation cover and green LAI increased as is the case of $fAPAR_{total}$. However, during the reproductive stage, the temporal patterns of $fAPAR_{total}$ and $fAPAR_{green}$ diverged markedly. With the decrease of green LAI, green vegetation fraction, leaf and canopy chlorophyll content, $fAPAR_{green}$ decreased, while $fAPAR_{total}$ showed relatively little decline. Consequently, in the reproductive stage, LUE_{green} in maize was much higher than LUE_{total} , and was not contaminated by the gradual senescence (Figure 4A). In soybean, the difference between $fAPAR_{total}$ and $fAPAR_{green}$ was smaller than in maize; LUE_{total} and LUE_{green} differed only in the late reproductive/senescence stage (Figure 4B).

Importantly, the reported behavior of LUE in all three definitions was consistent for eight years of observation despite differences in water management (irrigated vs. rainfed), weather conditions and crop hybrids (data not shown). Because LUE_{green} is not contaminated by varying greenness and light absorption, its

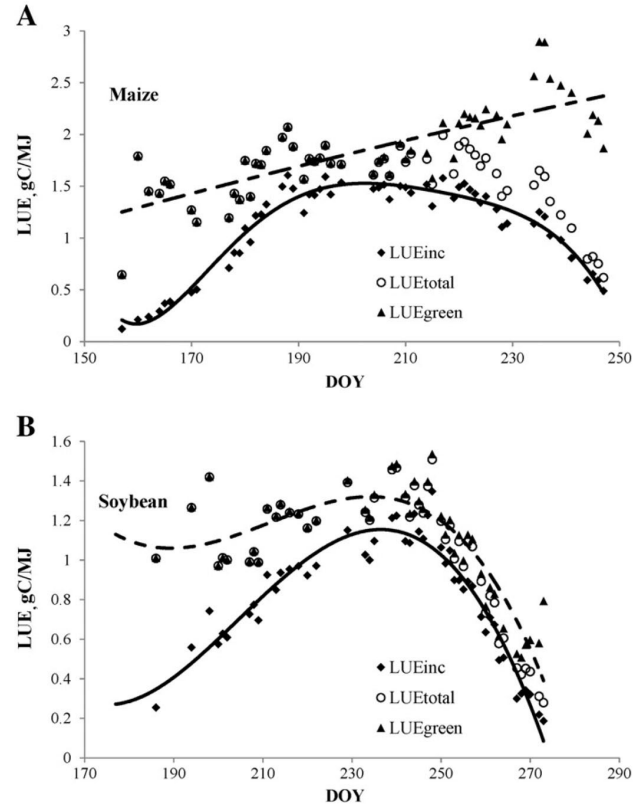


Figure 4. Temporal behaviors of light use efficiencies, LUE_{inc} , LUE_{total} and LUE_{green} , versus day of year (DOY) in maize (A) and soybean (B). Solid line is the seasonal change of LUE_{inc} , dashed line interval is the seasonal change of LUE_{green} .

properties are clearly different from the other two definitions and, thus, LUE_{green} provides the most mechanistically sound definition.

These different operational definitions of LUE have significant implications for the accuracy of GPP estimates when using different versions of the LUE model, as the different definitions of LUE can lead to large errors in calculated GPP. To illustrate, we calculated GPP for maize and soybean as $GPP = APAR_{green} \times LUE$, using all three LUE definitions: LUE_{inc} , LUE_{total} and LUE_{green} . GPP was estimated three ways, and the differences (δGPP) in percent between measured and calculated values, using the assumption of LUE_{green} as a reference, are presented in Figure 5. Note that since $\delta GPP = GPP - (APAR_{green} \times LUE_{green})$ is equal to zero, the errors are expressed relative to this baseline. In both crops, in vegetative stage the use of LUE_{inc} causes errors of approximately 90% in the beginning of the season, with minimal values (about 10%) in the middle of the season and 50% in the end. In the vegetative stage when vegetation is fully green, $fAPAR_{total} \cong fAPAR_{green}$ and the use of LUE_{inc} does not produce errors in GPP estimation. However, in the reproductive and senescent stages when the crop canopy is heterogeneous, errors of GPP estimation increased to approximately 50% by the end of the season. Consequently, the operational definition of the terms in the LUE model can have large implications for the accuracy of GPP values estimated in this way, and these errors vary temporally as the percentage of brown and green tissues change with phenology or ontogeny.

4. Conclusions

Clearly, the temporal behaviors of all three LUE definitions were very different, and these differences varied over time. In the two crops studied, LUE_{inc} followed a strong seasonal pattern that was strongly influenced by green LAI, canopy chlorophyll content and,

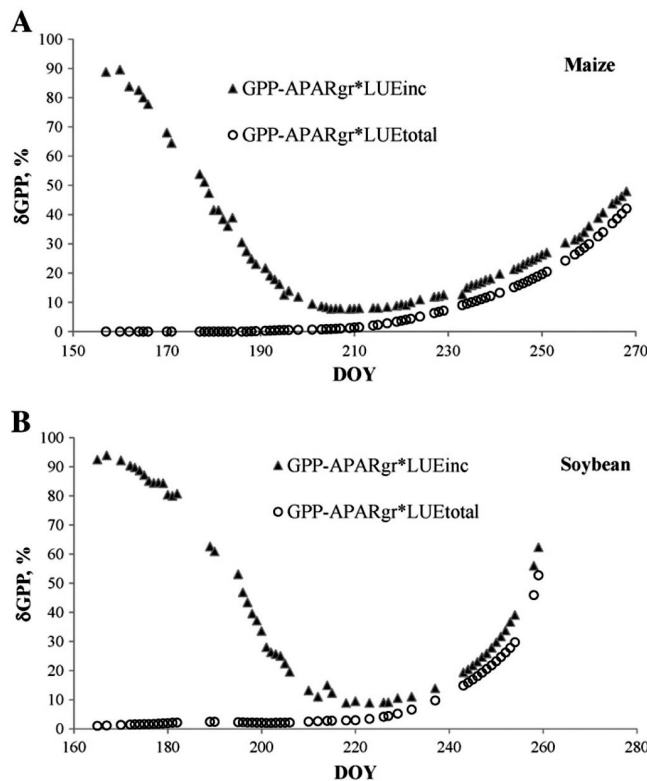


Figure 5. Errors of GPP estimation $\delta GPP = GPP_{meas} - GPP_{calc}$. GPP was calculated as $GPP = APAR_{green} \times LUE$, for light use efficiencies LUE_{inc} and LUE_{total} in maize (A) and soybean (B). Note that $GPP_{meas} = APAR_{green} \times LUE_{green}$, so $\delta GPP = GPP_{meas} - GPP_{calc}$ for LUE_{green} is equal to zero, and the errors are expressed relative to this baseline.

consequently, GPP. LUE_{total} oscillated around a near-constant value during the vegetative stage, depending mainly on plant physiological status (photosynthetic rate), PAR composition and magnitude (e.g. sunny vs. cloudy conditions), while in the reproductive stage it declined with green LAI and thus GPP. LUE_{green} varied 2- to 3-fold during the growing season with no clear seasonal pattern, while showing lots of day-to-day variability, and did not appear to be related to any biophysical characteristic studied; rather, it depended on the physiological status of vegetation, in response to PAR composition and magnitude as well as air temperature and soil moisture (not shown). Consequently, of the three LUE metrics, because GPP was normalized by $APAR_{green}$, LUE_{green} was least confounded by green canopy structure.

This contrasting LUE behavior illustrates that estimation of seasonal productivity could be different if different LUE definitions were used, as is the common practice in the literature (e.g., Garbulska, Penuelas, Gamon, Inoue and Filella, 2010; Hall et al., 1992; Lindquist et al., 2005; Monteith, 1972; Nichol et al., 2000; Norman and Arkebauer, 1991; Peng et al., 2011; Rosati and Dejong, 2003; Suyker et al., 2004). Furthermore, this behavior further varies over time with changing yellow/brown and green composition of the canopy, further confounding the interpretation of GPP calculations derived from this model. This simple analysis illustrates clear effects of seasonally changing canopy structure on the three definitions of the LUE model terms and consequently on any calculated GPP. Further analyses of vegetation stands having vastly different canopy structure, phenology, or environmental constraints on canopy growth and physiology would likely add additional complexity to these effects. While beyond the scope of our analyses, further studies of ecosystems from contrasting biomes with different

resource constraints (e.g. Garbulska, Penuelas, Gamon, et al., 2010) would likely reveal further causes of variability in LUE model behavior. Additionally, while not a focus of our analysis here, a more careful evaluation of how these different model definitions behave in a diurnal context would be illuminating.

The uncertainty estimates for GPP using different LUE definitions can be considered as a critical component of the total error budget in the context of remotely sensed based estimations of GPP. Thus, these findings have implications for the use of the LUE model by the remote sensing and carbon flux modeling communities. Clearly, more attention should be given to the operational definitions used, as the several definitions currently in use are not equivalent, and this can have large consequences for the estimated GPP. Better alignment with ground sampling methods, which may also have different operational definitions for the same model terms, should also be considered.

Given the findings here, we recommend the establishment of standard LUE definitions (e.g. using subscripts) that clarify the methodology used. We also recommend consideration of an LUE metric that is not confounded by changing pigmentation and green canopy structure during plant growth and senescence. The LUE_{green} , a ratio of GPP to PAR absorbed by photosynthetically active/green vegetation ($APAR_{green}$), best meets this requirement. However, green LAI used in calculation of LUE_{green} (Eq. (4)) represents a subjective metric, as it depends on a visual inspection, and interpretation of leaf color. While a strong linear relationship exists between canopy chlorophyll content and green LAI obtained using this subjective greenness attribute (Ciganda et al., 2008), this relationship exhibits hysteresis due to varying leaf chlorophyll content in heterogeneous canopies (Gitelson, Peng, Arkebauer and Schepers, 2014; Peng et al., 2011). For the same green LAI, total canopy chlorophyll content, which governs light absorption, may be much lower when leaf chlorophyll content decreases but leaves still look “green” and vertical distribution of chlorophyll content and green LAI inside the canopy becomes heterogeneous. This effect results in a strong overestimation of absorbed radiation $APAR_{green}$ and underestimation of LUE_{green} . A standard procedure for measurement of $APAR_{green}$ should be established and routinely used for accurate assessment of LUE_{green} . One challenge lies in the direct measurement of the proportion of green vegetation, which typically requires tedious and destructive sampling that is subject to error. A solution may lie in using spectral measurements such as greenness indices to assess this term. If properly measured, standardized and interpreted, the normalized difference vegetation index (NDVI) or other greenness indices could provide a rapid means to do this, as is currently done from satellite (Running et al. 2004; Gitelson, Peng, & Huemmrich, 2014), although further work is needed to standardize methodology and interpretation, particularly for field studies. Similar optical measurements of spectral reflectance or transmittance could be used to rapidly and non-destructively assess the green canopy portion (Serrano, Gamon, & Penuelas, 2000). The adoption of standard protocols and definitions for use in the LUE model would facilitate meta-analyses and better review the true underlying structural and physiological behavior of different ecosystems in response to changing conditions.

Acknowledgments — This research was supported by International Incoming Marie Curie fellowship (grant 623354) to A. Gitelson and NSERC and iCORE/AITF to J. Gamon. We sincerely appreciate the support provided by the Center for Advanced Land Management Information Technologies (CALMIT) and School of Natural Resources, and data from Carbon Sequestration Program, the University of Nebraska–Lincoln. Authors are thankful to four anonymous reviewers for constructive and helpful comments and criticism.

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